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LATE CRETACEOUS ANGIOSPERM WOODS FROM THE MCRAE FORMATION, SOUTH-CENTRAL NEW MEXICO, USA: PART 2

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Premise of research. Over the past 3 decades, angiosperm woods have been reported from the Campanian to the Maastrichtian of southern Laramidia, including Coahuila and Chihuahua, Mexico; Big Bend National Park, Texas; and the San Juan Basin, New Mexico. Recent investigations of the upper Campanian (76.5 to >72.5 Ma) Jose Creek Member of the McRae Formation, south-central New Mexico, indicate an abundance of well-preserved silicified woods, representing one of the most diverse Cretaceous wood floras in the world. In this report, we describe four new angiosperm wood types.

Methodology. The fossil woods described here were collected from the upper Campanian of south-central New Mexico, along the northeastern flank of the Caballo Mountains and in the adjacent Cutter Sag, and were studied using thin sections. The potential affinities of these McRae woods were determined by comparison with fossil and extant woods.

Pivotal results. The woods reported here comprise one magnoliid and three eudicots with varying levels of comparability to extant taxa. *Laurinoxylon rennerae* sp. nov. belongs to Lauraceae and has a combination of features found in multiple extant genera variously referred to as Cinnamomeae Nees, Laureae Maout & Decaisne, or Lauroideae Burnett/core Lauraceae. *Turneroxylon newmexicoense* gen. et sp. nov. is a eudicot with many similarities to Dilleniaceae but differs in having narrower rays. *Mcraeoxylon waddellii* gen. et sp. nov. has a suite of features seen in several families of Malpighiales, Myrtales, and Oxalidales. McRae angiosperm wood type 1 has a suite of features found in genera of Dilleniales, Ericales, and Malpighiales.

Conclusions. All wood types, with the exception of *M. waddellii*, have minimum axis diameters of >10 cm (12–50 cm), indicating that they represent trees. This reinforces previous evidence for the presence of small to large angiosperm trees in the Jose Creek Member and underscores the importance of woody angiosperms in vegetation of the southern Western Interior during the Campanian-Maastrichtian.

Keywords: angiosperm woods, Cretaceous, fossil wood, late Campanian, McRae Formation, New Mexico.

Introduction

The western margin of the former Western Interior Seaway preserves diverse Late Cretaceous floras, especially of Campanian and Maastrichtian age. Over the past 20 yr more than 40 new fossil angiosperm woods have been described from the southern Western Interior and adjacent regions of northern Mexico, including the San Juan Basin and Love Ranch Basin of New Mexico, the Big Bend region of Texas, and the Coahuila and Chihuahua states of northern Mexico. Some belong to genera that have multiple occurrences, e.g., *Paraphyllanthoxylon*, *Platanoxylon*, *Metcalfeoxylon*, and *Javelinoxylon* (e.g., Wheeler et al. 1994, 1995; Wheeler and Lehman 2000, 2009; Hudson 2006; Estrada-Ruiz et al. 2007, 2010, 2012*a*, 2012*b*; Estrada-Ruiz and Martínez-Cabrera 2011; García-Hernández et al. 2016). The relatively high diversity of angiosperm wood from these areas probably reflects warm subtropical to tropical temperatures during the Late Cretaceous and varied environments ranging from coastal to interior and from wet to semiarid (Lehman 1987; Wolfe and Upchurch 1987; Upchurch and Mack 1998; Upchurch et al. 1999, 2015; Wheeler and Lehman 2000; Estrada-Ruiz et al. 2012*a*).

In this article, we describe four new angiosperm wood types (a magnoliid and three eudicots) from the McRae Formation of south-central New Mexico (fig. 1). This is the second part of a comprehensive study of angiosperm woods from the McRae Formation and underlying Crevasse Canyon Formation of the Love Ranch Basin. These woods form part of a diverse macro-

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flora that includes abundant silicified conifer and angiosperm woods; silicified monocot axes; fern, gymnosperm, and angiosperm leaves; and gymnosperm and angiosperm reproductive structures. More than 40 species of woods and more than 100 species of leaves have been collected from the Jose Creek Member as a whole, including the fern *Woodwardia*; conifers belonging to the Araucariaceae, Cupressaceae, and possibly Pinaceae; monocots belonging to Araceae, Arecaceae, and possibly Pandanaceae; and diverse nonmonocot angiosperms belonging to Lauraceae, possibly Annonaceae, Nelumbonaceae, Platanaceae, Fagaceae, Celastraceae, and Myrtaceae (Upchurch and Mack 1998; Bogner et al. 2007; Estrada-Ruiz et al. 2011, 2012*a*, 2012*b*; Parrott and Upchurch 2017).

Material and Methods

Geologic Setting

The woods described in this article were collected from the Upper Cretaceous McRae Formation in south-central New Mexico (fig. 1), which represents the first basin fill in the Laramide Love Ranch Basin of south-central New Mexico (Seager et al. 1986, 1997; Amato et al. 2017). The formation is fluvial in origin and was deposited in an alluvial plain to piedmont environment, at least 200 km inland from the shoreline of the Western Interior Seaway (Molenaar 1983; Roberts and Kirschbaum 1995; Estrada-Ruiz et al. 2012*a*) at approximately 39° paleolatitude. Carbonaceous beds indicative of swamp conditions are virtually absent from the McRae Formation, in contrast to most units that yield Late Cretaceous macrofloras from the Western Interior.

The McRae Formation is divided into a lower Jose Creek Member and an upper Hall Lake Member. The Jose Creek Member and the lowermost part of the Hall Lake Member are now dated as late Campanian (Amato et al. 2017), rather than Maastrichtian, in contrast to earlier publications (Lozinsky et al. 1984; Upchurch and Mack 1998; Estrada-Ruiz et al. 2012*a*, 2012*b*). This new age is based on U-Pb dates from multiple horizons within the McRae Formation, including a volcanic clast from the base of the Jose Creek Member, three volcanic ashes that span the middle to upper Jose Creek Member, and a fourth volcanic ash from the lower part of the overlying Hall Lake Member. These dates range from 75.0 to 73.2 Ma. When accounting for statistical uncertainty ($\pm 2\ \sigma$), this places the Jose Creek Member in the age range of 76.1 to >72.5 Ma, older than the currently accepted age of 72.1 ± 0.2 Ma for the Campanian-Maastrichtian boundary (Cohen et al. 2013).

Methods

The woods described in this article were collected from multiple localities in the middle part of the Jose Creek Member as float, in stratigraphic sections where the source of the material could be constrained to the Jose Creek Member. Fossil woods were studied using thin sections. The woods were cut into blocks, glued to glass slides, sectioned, and ground until the details of internal anatomy were fully visible. The blocks and cover slips were affixed to slides using Norland optical adhesive type 72, which was polymerized for times ranging from half an hour with a sunlamp to overnight with an ultraviolet lamp. Thin sections were observed with two microscopes, a Zeiss photoscope I using brightfield optics, photographed with a Cannon Eos Digital Rebel XSi camera (12-megapixel resolution), and a Zeiss Axio Zoom.V16, photographed with a camera AxioCam MRc5 (5 megapixels) Zen 2012 (Blue Edition; Zeiss Efficient Navigation).

Descriptions and quantitative data follow recommendations of the International Association of Wood Anatomists (IAWA) list of microscopic features for hardwood identification (IAWA Committee 1989). For woods of Lauraceae, we use Richter's (1981, 1987) classification of vessel-ray parenchyma pits. Following the text description, we list the IAWA numerical codes of the features we observed in the wood. A v following a feature number indicates a tendency toward a feature or that it is of rare occurrence; e.g., 14v indicates that scalariform perforation plates are rare. A question mark after a feature number indicates that we were unable to determine whether that feature was present; e.g., 61? indicates we could not determine whether fiber pits were simple. Quantitative features were based on 25 measurements for each feature. We searched the InsideWood Database (InsideWood 2004–; Wheeler 2011) to create lists of modern and fossil taxa with anatomy similar to the McRae woods. The search criteria are listed in the discussion of each wood type, with feature numbers followed by the following codes: "p" for present, "a" for absent, "r" for required present, and "e" for required absent (i.e., excluded). We then consulted the literature on the woods with matching features (e.g., Metcalfe and Chalk 1950; Dickison 1967, 1979).

The fossil woods are housed in the Texas State University Paleobotanical Collections, San Marcos, Texas. Individual pieces of wood are given a specimen number preceded by the abbreviation TXSTATE. The slide number used for each illustration is given in the figure captions preceded by "S." Individual wood localities have a two-part number preceded by "Texas State University Paleobotanical Locality"; the number consists of the collection year (four digits) followed by a two-digit identifier. Specimens and locality data are archived in the Texas State University Paleobotanical Collections. Detailed locality data are not provided in this report because the localities occur on private land, and looting of fossil wood localities is common in the western United States.

Minimum axis diameter was calculated to determine possible growth habit for the fossil woods and provide data for future paleoecological studies. For nearly complete axes (i.e., axes rounded in cross section with a central nonwoody region), the maximum diameter of the actual axis was measured. For specimens that represented fragments of a much larger piece of wood, minimum axis diameter was estimated by calculating minimum radius and multiplying by 2. Minimum radius was calculated by aligning two rulers along the rays and measuring the distance from where the two rulers intersected to the distal edge of the specimen. When the measurements of the two rulers differed, the larger measurement was used to calculate minimum radius.

Because wood in the fossil record represents a mixture of branch wood, trunk wood, and root wood, a small diameter cannot be used by itself as an indicator of small stature. However, when there is an absence of anatomical features typical of vines and the minimum axis diameter exceeds 10 cm, we inferred tree habit. In forest ecology, 10-cm-diameter breast height is typically used as the cutoff between trees and saplings/shrubs.

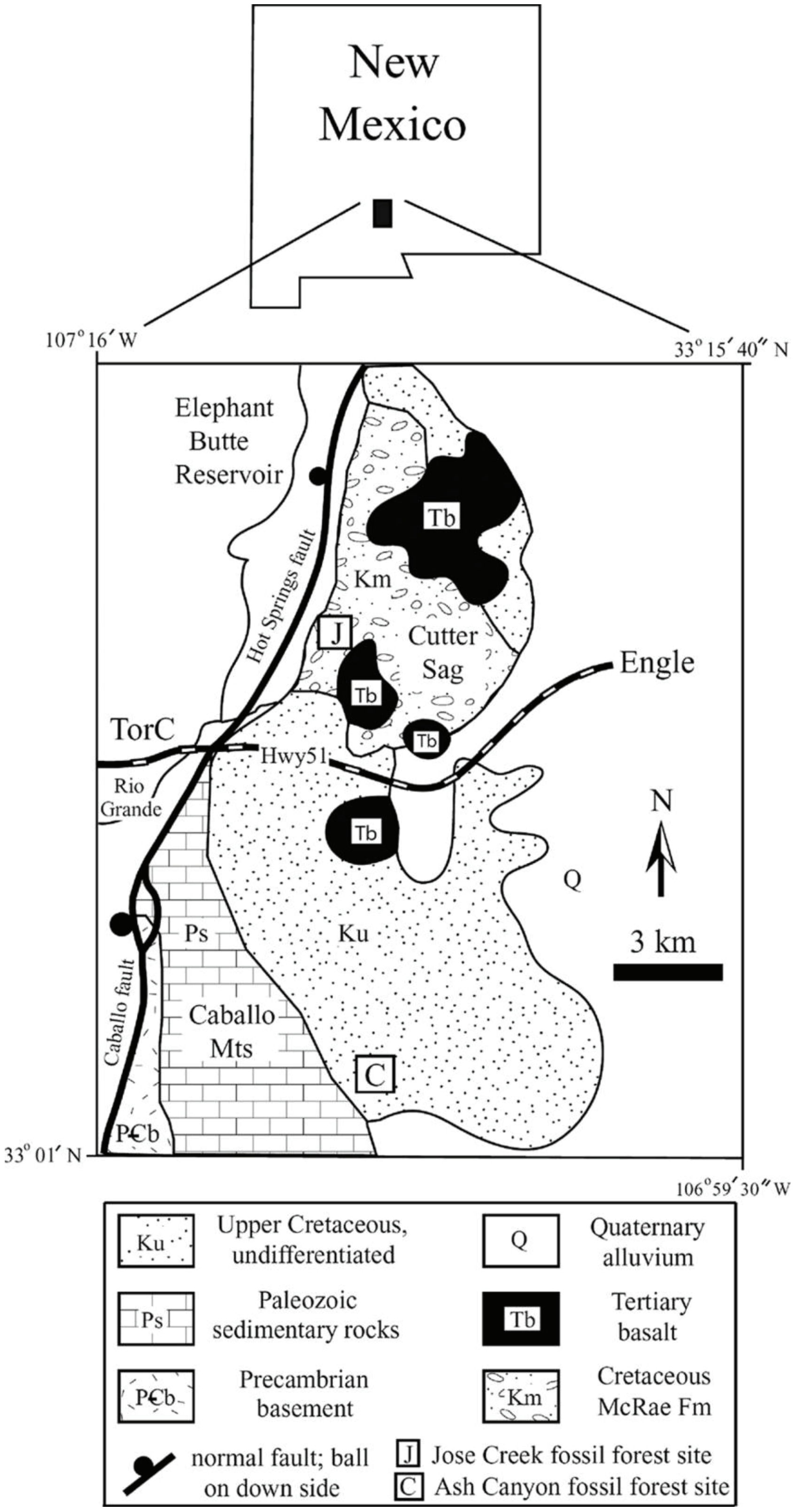

Fig. 1 Maps showing the location and geology of the study area.

Higher-level systematics follows APG IV (Angiosperm Phylogeny Group 2016). We use taxonomic names proposed by Chase and Reveal (2009) supplemented by informal names for well-corroborated clades. We present our taxonomic descriptions by the level of comparability to extant families, orders, and higher-level clades.

Results

Systematic Paleobotany

Magnoliids

Order—Laurales

Family—Lauraceae

*Genus—*Laurinoxylon *Felix*

*Species—*Laurinoxylon rennerae *Estrada-Ruiz, Wheeler, Upchurch, et Mack, sp. nov. (Fig. 2)*

Specific diagnosis. Growth rings indistinct, wood diffuse porous; vessels solitary and in radial multiples of 2 or 3 (up to 4); perforation plates predominantly simple, some scalariform with fewer than 10 bars per perforation plate; intervessel pits alternate and sometimes appearing opposite; vessel-axial parenchyma and vessel-ray parenchyma pits with reduced borders (Richter class b); fibers predominantly nonseptate, rarely septate; axial parenchyma scanty paratracheal to vasicentric; multiseriate rays up to 4 cells wide, heterocellular with 1 (or 2) marginal rows of upright and square cells; oil cells in the rays.

Etymology. In honor of Dr. Susanne Renner and in recognition of her contributions to the phylogeny of Lauraceae.

Holotype hic designatus. Specimen TXSTATE 1222.

Stratigraphic horizon. Jose Creek Member, McRae Formation.

Locality. Texas State University Paleobotanical Locality 1991-15/16.

Age. Late Campanian.

Description in IAWA feature numbers. 2, 5, 13, 14v, 15v, 22, 23, 25, 31, 32, 41, 47, 52?, 53?, 54?, 56, 61? 62? 65v, 66, 69, 78, 79v, 92, 98, 106, 107v, 115, 124.

Description. Description based on one sample. Growth rings indistinct to absent. Wood diffuse porous. Vessels solitary (36%) and in radial multiples of 2 or 3 (4); circular to oval in outline (fig. 2*A*, 2*B*); mean tangential vessel diameter 84 μm (range = 40–136, SD = 21.6), and 19 vessels/mm^2 (range = 13–26, SD = 4.3; fig. 2*A*); perforations simple (fig. 2C) and rarely scalariform with fewer than 10 bars (fig. 2*D*, arrow); intervessel pitting medium (8–10 μm), alternate and rarely appearing opposite, polygonal in outline, with elliptical apertures (fig. 2*C*); vessel-axial parenchyma and vessel-ray parenchyma pitting with reduced borders, pits vertically and horizontally elongate (scalariform, gash-like) to round (Richter class b; fig. 2*D*, 2*E*); abundant thin-walled tyloses present (fig. 2*D*, 2*F*). Axial parenchyma apotracheal diffuse and scanty paratracheal to vasicentric (fig. 2*B*), usually 3–6 cells per axial parenchyma strand. Rays multiseriate, 2–4 cells wide, uniseriate rays rare (fig. 2*F*), rays heterocellular with procumbent body cells and usually 1 or 2 marginal rows of square cells (fig. 2*F*, 2*G*), rarely more, up to 4 marginal rows; multiseriate rays 5–34 cells high, and 396 μm high (range = 155–888, SD = 169). Rays 9 per millimeter (range = 7–12; fig. 2*F*). Oil cells generally in the ray margins, barrel shaped (fig. 2*G*, arrows). Fibers, nonseptate and very rarely septate, with medium-thick walls, pitting not observed (fig. 2*F*).

Remarks. This wood has a combination of features restricted to Lauraceae (Richter 1981, 1987). We searched the InsideWood Database for diffuse porous wood (5p), simple perforation plates (13p) and scalariform perforation plates with fewer than 10 bars (14p, 15p), alternate intervessel pitting (22p), vessel-ray parenchyma pits with reduced borders (32p), nonseptate fibers (66p), scanty paratracheal parenchyma (78p), but not aliform to confluent or banded parenchyma (80e, 83e, 85e, 86e), rays mostly 3 or 4 seriate (absence of exclusively 1 seriate and >10 seriate; 96e, 99e) generally with 1–4 rows of upright cells (absence of homocellular rays: 104e, 105e; absence of >4 rows of upright cells: 108a), and oil cells in rays (124r). This combination of characters returned species of these lauraceous genera: *Aspidostemon*, *Endlicheria*, *Laurus*, *Lindera*, *Litsea*, *Machilus*, *Nectandra*, *Neolitsea*, and *Ocotea*. Of these genera, only *Laurus*, *Lindera*, and *Litsea* have species with oil cells only associated with ray parenchyma. These three genera are in a group variously referred to as Cinnamomeae Nees, Laureae Maout & Decaisne, or Lauroideae Burnett/core Lauraceae (Stevens 2001–).

As Page (1967) noted, using the name *Ulminium* for lauraceous wood is unfortunate, because that name suggests affinities with the Ulmaceae. However, *Ulminium* Unger 1842 has nomenclatural priority over *Laurinoxylon* Felix 1883. Recently, Doweld (2017) formally proposed that *Laurinoxylon* Felix be conserved over *Ulminium* as a name for fossil lauraceous woods. There have been earlier suggestions that *Laurinoxylon*, rather than *Ulminium*, be used (e.g., Süss 1958). Although Doweld's proposal has not been formally accepted, we agree with Doweld's argumentation and are using *Laurinoxylon*.

Dupéron et al. (2008, p. 1) examined Unger's original material and proposed an emended diagnosis of *Laurinoxylon* (Unger): "heteroxylous fossil wood with average sized solitary vessels or in radial groups; perforation plates simple and sometimes scalariform; intervascular pits alternate and moderately large; thyloses [sic] present. Paratracheal parenchyma. Uni to five seriate rays, slightly heterocellular and less than 1 mm high; ray-vessel pits large often stretched. Libriform or with radial pits fibres. Oil cells or mucilage (idioblasts) present." Mantzouka et al. (2016) suggested that idioblast location is important for creating groups of *Laurinoxylon* species. Because idioblasts in this McRae wood only occur associated with ray parenchyma, it falls into their type 1 group (oil cells only associated with rays).

Woods of Lauraceae are common in the fossil record (Dupéron-Laudoueneix and Dupéron 2005; Gregory et al. 2009). Woods with characteristics of *Laurinoxylon*, some under the name of *Ulminium*, have been reported from the Cretaceous of North America, Europe, and Asia and the Paleogene of North America, Europe, and South America (e.g., Page 1967; Romero 1970; Wheeler et al. 1977; Crawley 1989; Brea 1995; Wheeler and Manchester 2002; Philippe et al. 2008; Gregory et al. 2009). Of the Cretaceous woods with features of *Laurinoxylon*, only *Ulminium kokubunii* has the combination of simple and scalari-

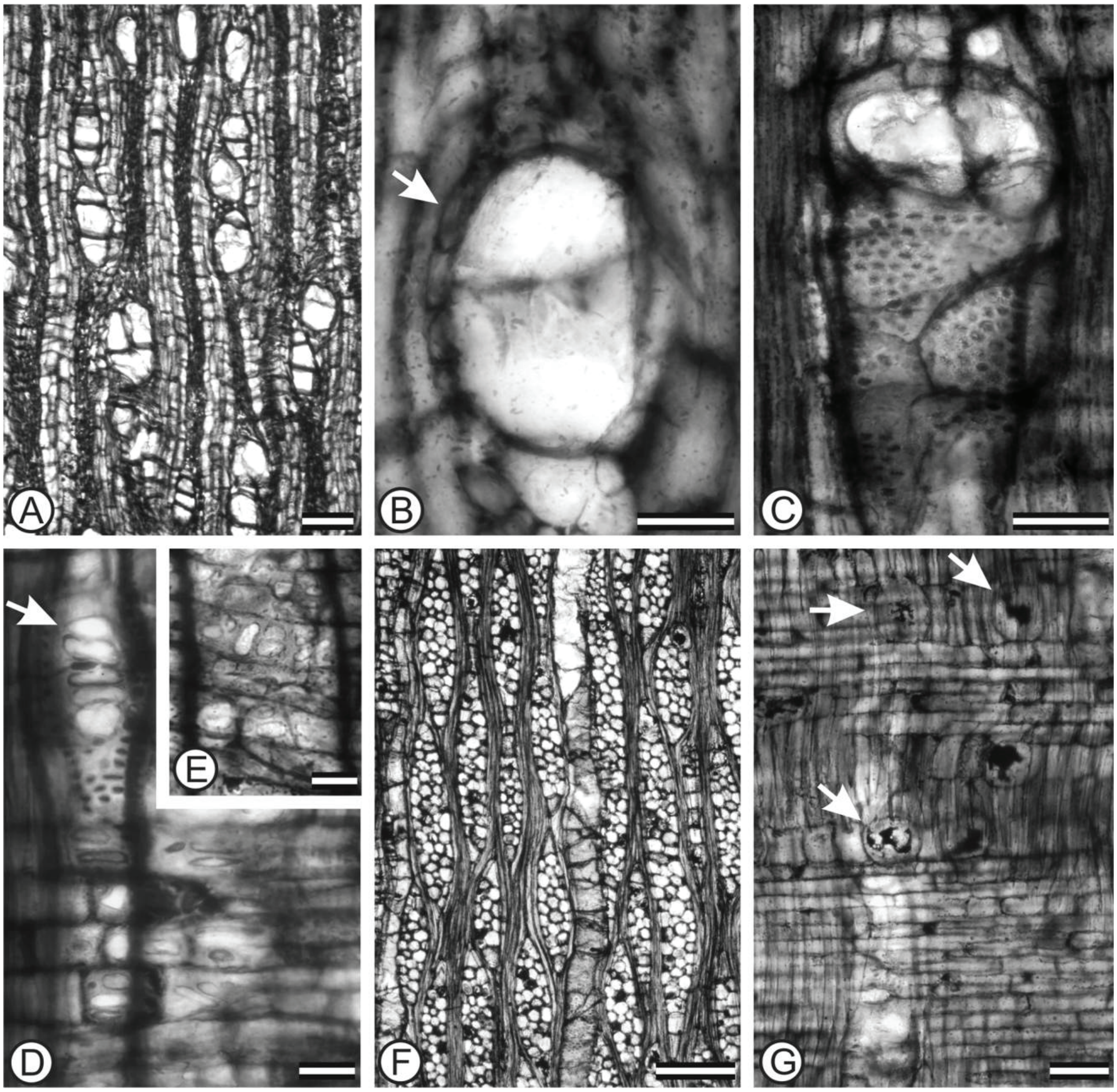

Fig. 2 *Laurinoxylon rennerae* Estrada-Ruiz, Wheeler, Upchurch, et Mack, sp. nov. Holotype (TXSTATE 1222) Lauraceae. *A*, Transverse section (TS). Diffuse porous wood with vessels solitary and in radial multiples. TXSTATE 1222–S1. Scale bar = 104 μm. *B*, TS. Scanty paratracheal parenchyma (arrow). TXSTATE 1222-S1. Scale bar = 35 μm. *C*, Radial longitudinal section (RLS). Simple perforation plate and crowded alternate intervessel pits. TXSTATE 1222-S9. Scale bar = 45 μm. *D*, RLS. Scalariform perforation plate (arrow) and horizontally elongate vessel-ray parenchyma pits with reduced borders, tyloses in vessel. TXSTATE 1222-S9. Scale bar = 33 μm. *E*, RLS. Vessel-ray parenchyma pits with reduced borders. TXSTATE 1222-S9. Scale bar = 23 μm. *F*, Tangential longitudinal section. Multiseriate rays, tyloses in vessel. TXSTATE 1222-S6. Scale bar = 145 μm. *G*, RLS. Heterocellular rays, procumbent body cells and square to upright marginal cells, oil cells common in ray margins (arrows). TXSTATE 1222-S10. Scale bar = 72 μm.

form perforation plates (table 1). *Ulminium kokubinii* differs from *L. rennerae* in having distinct growth rings, semi-ring-porosity, rays only up to 3 cells wide, oil cells associated with axial parenchyma, and predominantly homocellular rays (Takahashi and Suzuki 2003). We propose the new combination *Laurinoxylon kokubunii* (Takashi et Suzuki) Estrada-Ruiz, Wheeler, Upchurch, et Mack, comb. nov.

The minimum axis diameter of the holotype is 50 cm. This indicates that the parent plant was a tree, like most extant Lauraceae.

Eudicots

?Dilleniales

Genus—Turneroxylon *gen. nov. Estrada-Ruiz, Wheeler, Upchurch, et Mack, gen. nov. (Fig. 3)*

Type Species—Turneroxylon newmexicoense *Estrada-Ruiz, Wheeler, Upchurch, et Mack, sp. nov.*

Etymology. In honor of Ted Turner, owner of the Armendaris Ranch, locality of the fossil wood, and in recognition of his numerous contributions to the conservation of plant and animal species.

Generic diagnosis. Growth rings indistinct, wood diffuse porous; predominantly solitary vessels, rarely in multiples of 2; perforation plates exclusively scalariform. Intervessel pits mostly opposite, sometimes scalariform; vessel-ray parenchyma pits mostly with distinct borders, some horizontally elongate with reduced borders; axial parenchyma apotracheal, diffuse and rarely diffuse in aggregates; nonseptate fibers with distinctly bordered pits, vasicentric tracheids present; rays heterocellular, uniseriate, and multiseriate (>4 seriate), tending to 2 distinct sizes.

Type species. *Turneroxylon newmexicoensis*.

Etymology. Referring to the state of New Mexico, where the fossil was collected.

Synonymy. Ericales type 1, Estrada-Ruiz et al. 2012*b*, fig. 5*A*, 5*B*.

Specific diagnosis. As for genus.

Holotype hic designatus. Specimen TXSTATE 1213.

Stratigraphic horizon. McRae Formation, Jose Creek Member.

Locality. Texas State University Paleobotanical Locality 1991-17.

Age. Late Campanian.

Description in IAWA feature numbers. 2, 5, 9, 14, 16, 17, 30, 31, 32, 41, 47, 54, 56, 60, 62, 63, 66, 76, 77v, 98, 103v, 106, 107, 108, 115.

Description. Description based on one specimen. Growth rings indistinct to absent. Wood diffuse porous. Vessels predominantly solitary (>90%; fig. 3*A*, 3*B*), oval in outline. Mean tangential diameter 80 μm (range = 56–100, SD = 11), and 14 vessels/mm^2 (range = 8–22, SD = 3.6). Perforation plates scalariform, with 21 bars per plate (range = 13–31, SD = 5), some bars forked (fig. 3*C*). Intervessel pits not observed. Vessel-ray parenchyma pits with both distinct borders and reduced borders (round to horizontally elongate shape; fig. 3*D*, 3*E*, arrows). Mean vessel element length 844 μm (range = 560–1480, SD = 202). Tyloses present, bubble-like (fig. 3*F*). Axial parenchyma apotracheal, diffuse and rarely diffuse in aggregates (fig. 3*A*, 3*B*), over 5 cells per axial parenchyma strand. Rays heterocellular, uniseriate, and multiseriate, tending to 2 distinct sizes (fig. 3*G*). Uniseriate rays with square and procumbent cells in the body, 2–30 cells high, and 466 μm high (range = 24–1272, SD = 271.5). Multiseriate rays with procumbent cells in the body, usually 1–2 marginal rows (up to 7) with square to upright marginal cells (fig. 3*G*, 3*I*). Body of multiseriate rays is generally 3–6 (–8) cells wide, 70 μm wide (range = 24–96, SD = 17.5), multiseriate rays 10–42 cells high, 545 μm high (range = 192–1008, SD = 206). Rays 6–15 per millimeter. Fibers nonseptate, with walls of medium thickness (fig. 3*F*) with distinctly bordered pits in tangential and radial walls. Vasicentric tracheids with 1 row of bordered pits, pits visible in both tangential and radial sections (fig. 3*H*).

Remarks. *Turneroxylon newmexicoense* has many of the features that characterize woods of extant Dilleniaceae. These include the presence of diffuse porous wood (5p) with more than 90% solitary vessels (9p) that are randomly arranged (6a, 7a, 8a), scalariform perforation plates (14p) with fewer than 50 bars per plate, vessel-ray parenchyma pits with distinct borders (30p) and also with reduced borders (31p, 32p) vasicentric tracheids (60p), and multiseriate rays more than 4 cells wide (98p). This suite of features is present in the subfamilies Dillenioideae (e.g., *Dillenia*) and Delimioideae (*Tetracera*; Dickison 1967, 1979; InsideWood 2004–). Both subfamilies

Table 1

Comparison of Select Cretaceous Northern Hemisphere *Laurinoxylon* Species

Species	RMs	VTD	V/mm^2	PP	VRP	Septate fibers	Oil cells	RW
Laurinoxylon pattersonensis[a]	5	82–116	<20	Simple	Large, horizontally elongate	Yes	Rays	Up to 3
Laurinoxylon mulleri[a]	4	81–127	<20	Simple	?	Yes	Rays	Up to 4
Laurinoxylon (Page Group XIA)[b, c]	4	58–98	<40	Simple	Reduced borders, simple	Yes	Rays, among fibers	Up to 3
Laurinoxylon kokubunii[d]	4	45–115	24–32	Simple and scalariform	Alternate, simple and round	Yes	Axial parenchyma	Up to 3
Laurinoxylon rennerae	4	40–136	13–26	Simple and scalariform	Round, vertically and horizontally elongate	Yes	Rays	Up to 4

Note. RMs = maximum number of vessels in a radial multiple; VTD = range tangential vessel diameter in μm; V/mm^2 = vessel elements per square millimeter; PP = perforation plate type; VRP = vessel-ray parenchyma pits; RW = ray width in cell number. Underlined = *Laurinoxylon rennerae*.

[a] (Page) Prakash et Tripathi 1974.

[b] Page 1980.

[c] InsideWood 2004–.

[d] (Takahashi and Suzuki) Estrada-Ruiz, Wheeler, Upchurch et Mack; this article.

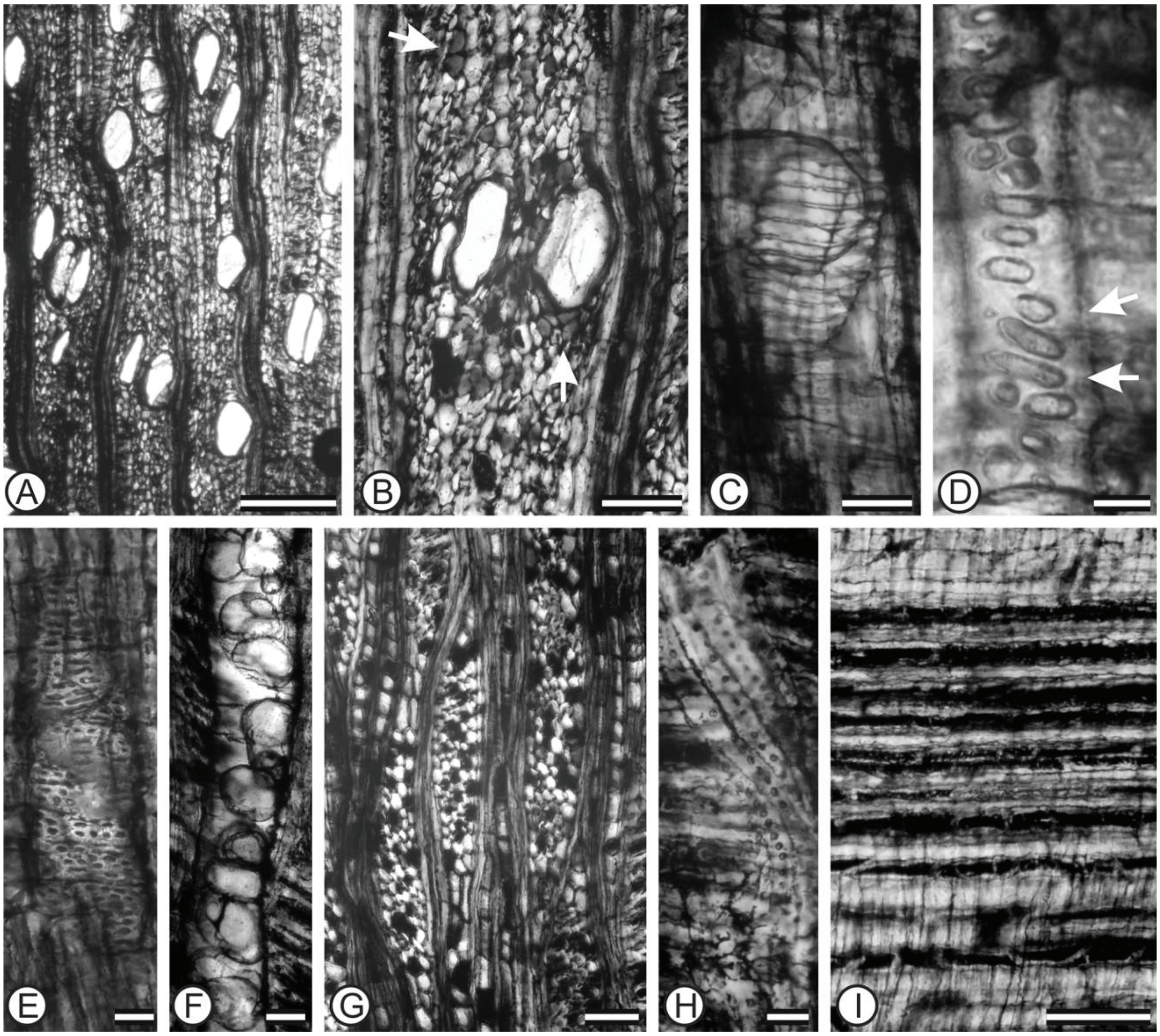

Fig. 3 *Turneroxylon newmexicoensis* Estrada-Ruiz, Wheeler, Upchurch, et Mack, gen. et sp. nov. Holotype (TXSTATE 1213). *A*, Transverse section (TS). Diffuse porous wood with solitary vessels, overlapping end walls giving appearance of vessel pairs. TXSTATE 1213-S3. Scale bar = 200 μm. *B*, TS. Solitary vessels, diffuse axial parenchyma (arrows). TXSTATE 1213-S3. Scale bar = 70 μm. *C*, Tangential longitudinal section (TLS). Scalariform perforation plate, some bars are forked. TXSTATE 1213-S10. Scale bar = 48 μm. *D*, Radial longitudinal section (RLS). Vessel-ray parenchyma pits with reduced borders, some appearing simple (arrows). TXSTATE 1213-S10. Scale bar = 12.5 μm. *E*, RLS. Vessel-ray parenchyma pits with distinct borders. TXSTATE 1214-S6. Scale bar = 23 μm. *F*, TLS. Tyloses, bubble-like. TXSTATE 1213-S4. Scale bar = 56 μm. *G*, TLS. Multiseriate rays, composed of cells of varying shapes, some cells with dark contents. TXSTATE 1213-S4. Scale bar = 100 μm. *H*, TLS. Vasicentric tracheids with one row of bordered pits. TXSTATE 1213-S4. Scale bar = 30 μm. *I*, RLS. Heterocellular ray with procumbent cells in the body. TXSTATE 1213-S9. Scale bar = 105 μm.

also have axial parenchyma that is diffuse and diffuse in aggregates. The most notable difference between our fossil and the extant subfamilies Dillenioideae and Delimioideae is ray size. In *Turneroxylon*, the rays tend to be of two distinct sizes, and the maximum ray width is 8 cells. In Dillenioideae and Dilimioideae, the rays obviously are of two distinct sizes, and the multiseriate rays are 10 or more cells wide (Dickison 1967, 1979; InsideWood 2004–).

Among fossil woods from the Western Interior, *T. newmexicoense* is most similar to DB.D1 Xylotype 2 from Paleocene of the Denver Basin (Wheeler and Michalski 2003). DB.D1 Xylotype 2 differs from *Turneroxylon* in having more bars per perforation plate (22–45 bars), rays clearly of two distinct sizes, and sheath cells (table 2).

Page (1979, 1980, 1981) created groupings, based on anatomical features, for the Californian Maastrichtian woods she studied. *Turneroxylon* falls into her group IIIB. Pores mostly solitary, perforations scalariform, bars averaging fewer than 50. Parenchyma mostly apotracheal. She further divided that group based on intervessel pits, a feature we did not observe.

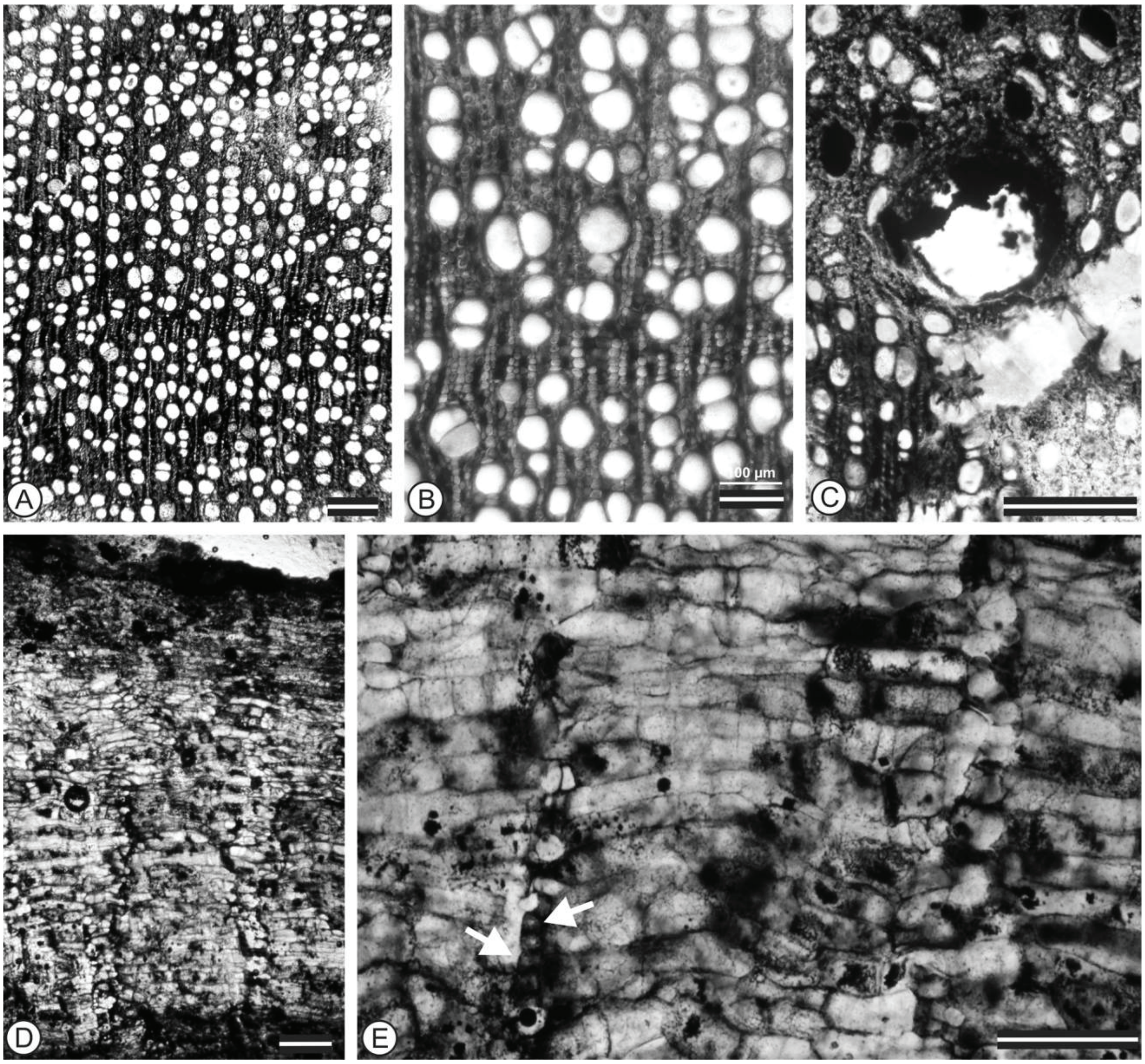

Fig. 4 *Macraeoxylon wadellii* Estrada-Ruiz, Wheeler, Upchurch, et Mack, gen. et sp. nov. Holotype (TXSTATE 1201) and paratype (TXSTATE 1225). *A*, Transverse section (TS). Growth rings indistinct, diffuse porous wood. TXSTATE 1201-S1. Scale bar = 200 μm. *B*, TS. Solitary vessels rounded in outline, and diffuse axial parenchyma. TXSTATE 1201-S1. Scale bar = 100 μm. *C*, TS. Cavities probably representing root penetration. TXSTATE 1201-S2. Scale bar = 250 μm. *D*, Bark. TXSTATE 1225-S1. Scale bar = 176 μm. *E*, TS. Detail of the bark showing different types of cells and apparently fibers (arrows). TXSTATE 1225-S1. Scale bar = 140 μm.

None of the 12 specimens she assigned to her group IIIB are comparable to *Turneroxylon*. CASG 60122, CASG 60125, CASG 60127, CASG 60128, CASG 60129, CASG 60131, CASG 60132, CASG 60133, CASG 60134, CASG 60206, and CASG 60207 differ because they do not have vasicentric tracheids; they also differ in some ray features (width, cellular composition). CASG 60135 has vasicentric tracheids, but its rays are only 2 or 3 cells wide, and perforation plates have fewer than 15 bars.

The minimum axis diameter of *T. newmexicoense* is difficult to estimate because some parts of the sample are twisted. The holotype represents an angular fragment from one side of a large axis and measures approximately 5 cm × 6 cm in cross section. Estimates of its minimum axis diameter range from 12 to 24 cm, indicating *Turneroxylon* was a tree.

Core Eudicots

Order and Family—Uncertain

Genus—Mcraeoxylon *gen. nov. Estrada-Ruiz, Wheeler, Upchurch, et Mack, gen. nov. (Figs. 4, 5)*

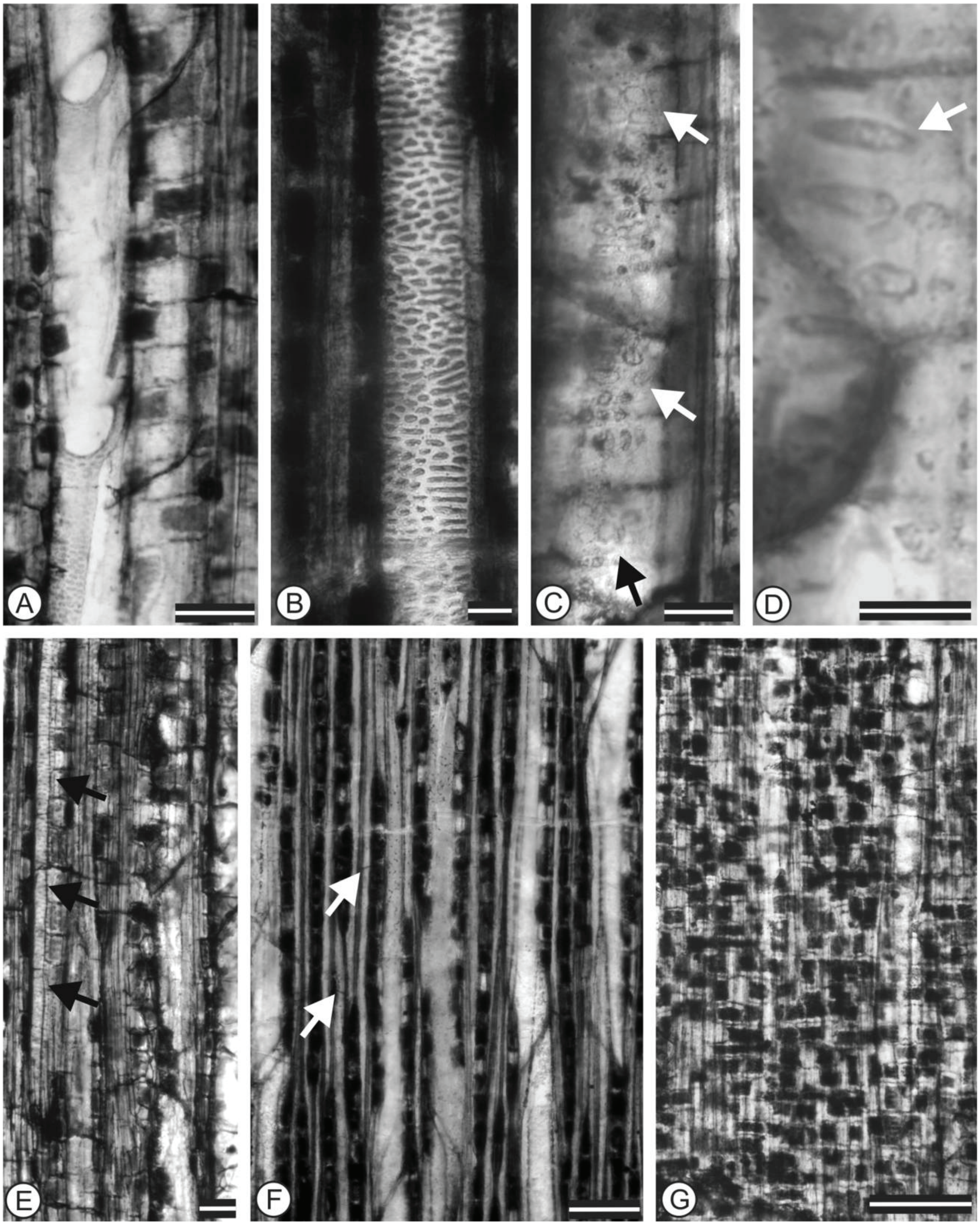

Fig. 5 *Macraeoxylon wadellii* Estrada-Ruiz, Wheeler, Upchurch, et Mack, gen. et sp. nov. Holotype (TXSTATE 1201) and paratype (TXSTATE 1225). *A*, Radial longitudinal section (RLS). Simple perforation plates. TXSTATE 1201-S13. Scale bar = 50 μm. *B*, Tangential longitudinal section (TLS). Alternate to scalariform intervessel pits. TXSTATE 1201-S14. Scale bar = 20 μm. *C*, RLS. Vessel-ray parenchyma pits with reduced borders (arrows). TXSTATE 1201-S13. Scale bar = 40 μm. *D*, RLS. Vessel-ray parenchyma pits with elongated shape (arrow). TXSTATE 1201-S13. Scale bar = 16 μm. *E*, TLS. Axial parenchyma strand (arrows). TXSTATE 1201-S13. Scale bar = 60 μm. *F*, TLS. Uniseriate rays and septate fibers (arrows). TXSTATE 1201-S14. Scale = 80 μm. *G*, RLS. Heterocellular ray with intermixed upright, square, and procumbent cells. TXSTATE 1201-S13. Scale bar = 130 μm.

Table 2

Comparison between *Turneroxylon newmexicoense* and DB.D1Xylotype 2 from Denver Basin

Features	DB.D1Xylotype 2	*Turneroxylon newmexicoense*
RMs	Up to 2	Up to 2
TVD	93	80 (56–100) μm
V/mm^2	8–14	8–22
Bars/PP	22–45	13–31
Intervessel pits	Not observed	?Opposite to some scalariform
V-RPP	?Distinct to reduced borders	Distinct to reduced borders
APAR	Rare	Apotracheal diffuse to diffuse in aggregates
Vasicentric tracheids	Present	Present
Sheath cells	Present	?
URH	...	2–30 cells and 24–1272 μm high
MSRW	4–8 cells	3–6 cells and 24–96 μm wide
MSRH	847 μm high	10–42 cells and 192–1008 μm high

Note. RMs = maximum number of vessels in a radial multiple; VTD = tangential vessel diameter; V/mm^2 = vessel elements per square millimeter; B/PP = number of bars per scalariform perforation plate; VRP = vessel-ray parenchyma pits; APAR = axial parenchyma; URH = uniseriate ray height; MSRW = width of multiseriate rays; MSRH = multiseriate ray height.

Type Species—Mcraeoxylon waddellii *Estrada-Ruiz, Wheeler, Upchurch, et Mack, sp. nov.*

Etymology. Referring to the McRae Formation, where the fossil wood was collected.

Generic diagnosis. Growth rings indistinct; vessels solitary and in short radial multiples, perforation plates simple; intervessel pits alternate to scalariform; vessel-ray parenchyma pits with reduced borders; axial parenchyma rare, some apotracheal diffuse; septate and nonseptate fibers; rays heterocellular, predominantly uniseriate, rarely biseriate.

Type Species—Mcraeoxylon waddellii *Estrada-Ruiz, Wheeler, Upchurch, et Mack, sp. nov.*

Etymology. In honor of Tom Waddell, manager of the Armendaris Ranch, the source of the fossil wood, and in recognition of his invaluable assistance.

Synonymy. Malpighiales, Estrada-Ruiz et al. 2012*b*, fig. 5*E*, 5*F*.

Specific diagnosis. As for genus.

Holotype hic designatus. Specimen TXSTATE 1202.

Paratype hic designatus. Specimen TXSTATE 1225.

Stratigraphic horizon. McRae Formation, Jose Creek Member.

Locality. Texas State University Paleobotanical Locality 1992-01, float below Fossil Forest Bed.

Age. Late Campanian.

Description in IAWA feature numbers. 2, 5, 13, 20, 21v, 22, 24, 25, 26, 27, 31, 32, 41, 49, 53, 61?, 62?, 65, 66, 69, 75, 76v, 96, 97v, 109, 115, 116.

Description. Description based on two samples of wood (fig. 4*A*–4*D*) and the remains of bark tissue (fig. 4*D*, 4*E*). Growth rings indistinct to absent. Wood diffuse porous. Vessels solitary, and occasionally in radial multiples of 2 or 3 (fig. 4*A*, 4*B*). Mean tangential diameter of 58 μm (range = 25–88), and 67 vessels/mm^2 (range = 44–83). Simple perforation plates (fig. 5*A*), intervessel pits alternate to scalariform (fig. 5*B*); vessel-ray parenchyma pits round to oval and horizontally elongated with reduced borders (fig. 5*C*, 5*D*). Mean vessel element length 420 μm (range = 280–616, SD = 86.7). Tyloses present in some vessels. Axial parenchyma rare, apotracheal diffuse (figs. 4*A*, 4*B*, 5*E*), strands of axial parenchyma >6 cells long (fig. 5*E*). Rays heterocellular, predominantly uniseriate (fig. 5*F*), rarely biseriate; uniseriate rays 11 cells (range = 2–28) and 342 μm high (range = 112–776); rays composed of intermixed upright, square, and barely procumbent cells (fig. 5*G*). Rays abundant, 18–27 per millimeter (fig. 5*F*). Fibers with medium-thick walls, septate and nonseptate (fig. 5*E*, 5*F*); pits not observed. Randomly distributed cavities present in the wood and periderm (fig. 4*C*, 4*D*), source uncertain. Bark consisting of elongate thin-walled cells arranged in radial files (fig. 4*D*, 4*E*) that are intermixed with isodiametric cells (fig. 4*E*) and some fibers (fig. 4*E*, arrows).

Remarks. This wood has a combination of characteristics uncommon in fossil woods from the Campanian-Maastrichtian of western North America: indistinct growth rings (2p), diffuse porosity with vessels solitary and in short radial multiples (5p, 6a, 7a, 8a, 9a, 10a, 11a, 12a), simple perforation plates (13p), alternate intervessel pitting that is not minute (22p, 24a), vessel-ray pitting with reduced borders (31p), septate and nonseptate fibers (65p, 66p), rare axial parenchyma (75p), nonstoried narrow rays, mostly uniseriate, occasionally biseriate, over 10 rays per millimeter (98a, 99a, 116p, 118a).

Among extant angiosperms, this combination of features occurs in seven families of core eudicots: Achariaceae, Hypericaceae, Phyllanthaceae, and Salicaceae of the Malpighiales; Lythraceae and Melastomataceae of the Myrtales; and Elaeocarpaceae of the Oxalidales. Determining the relationships of this wood to a single family or order does not seem possible at this time. Problems with this wood mimic those that Page (1981) encountered when working with the small-diameter axes from the Maastrichtian of California. This McRae wood is a small axis (juvenile wood); the bulk of information on wood anatomy is for mature wood of trees and large shrubs. This plant's living relatives may be ones whose anatomy has never been described.

Among fossil angiosperms, this particular combination of features (i.e., indistinct growth rings, diffuse porosity, simple perforation plates, vessel-ray pitting with reduced borders, septate and nonseptate fibers, rare axial parenchyma and uniseriate rays) occurs in *Fulleroxylon armendarisense* Estrada-Ruiz et al. from the McRae Formation, New Mexico (Estrada-Ruiz et al. 2012*a*). *Fulleroxylon armendarisense* differs from *Mcraeoxylon* in having vessels with a tendency to be of two distinct diameter classes, tyloses common in wide vessels, segmented and bubble-like, and vasicentric tracheids (Estrada-Ruiz et al. 2012*a*).

The holotype is the larger axis and measures 2.4 cm × 3 cm in diameter. Growth habit of the source plant of this wood type is unknown because these small-diameter axes could represent shrubs, early stages of growth or branches of trees, or a vine without the syndrome of two distinct sizes of vessels.

Order and Family—Uncertain

McRae Angiosperm Wood Type 1 (Fig. 6)

Synonymy. Ericales type 2, Estrada-Ruiz et al. 2012*b*, fig. 5*C*, 5*D*.

Studied specimens. TXSTATE 1214, 1224.

Stratigraphic horizon. McRae Formation, Jose Creek Member.

Locality. Texas State University Paleobotanical Locality 1991-13.

Age. Late Campanian.

Description in IAWA feature numbers. 2, 5, 9, 14, 17, 20v, 21, 30, 40, 41, 48, 49, 54, 60, 62, 66, 69, 76, 98, 102, 109, 116.

Description. Description, mean values, and ranges of vessel diameter and density based on two specimens. Growth rings indistinct to absent. Wood diffuse porous. Vessels predominantly solitary (>90%; fig. 6*A*, 6*B*), round to oval in outline. Vessel diameter difficult to measure because of compression of the sample (fig. 6*A*); mean tangential diameter 68 μm (range = 16–112, SD = 19.5); 36 vessels/mm^2 (range = 22–63, SD = 8). Perforation plates scalariform, 32 bars per plate (range = 24–44, SD = 6), some bars forked (fig. 6*C*, 6*D*). Intervessel pitting opposite, 4–8 μm across, sometimes scalariform pits at the ends of vessel elements (fig. 6*D*). Vessel-ray parenchyma pits with distinct borders (fig. 6*E*, 6*F*). Mean vessel element length 905 μm (range = 464–1520, SD = 229). Tyloses not observed, some vessels with yellow deposits. Axial parenchyma mostly apotracheal diffuse (fig. 6*A*, 6*B*). Some parenchyma strands with small pits visible in longitudinal section, more than 5 cells per axial parenchyma strand. Rays heterocellular, uniseriate, and multiseriate (fig. 6*G*, 6*H*, 6*J*). Uniseriate rays with intermixed procumbent and square cells, ray height 2–12 cells and 309 μm (range = 112–664, SD = 170). Multiseriate rays 2–6 (–9) seriate, generally with intermixed procumbent and square cells in the body, 1 to more than 4 rows of square to upright marginal cells (fig. 6*G*). Multiseriate rays, aggregated in some parts of the wood, maybe in response wounding. Body of multiseriate rays 59 μm wide (range = 20–100, SD = 19.5), multiseriate rays 12–53 cells high, and 951 μm high (range = 384–2176, SD = 474). Rays abundant, 14–20 per millimeter. Septate and nonseptate fibers, with walls of medium thickness. Fibers with 1 or 2 rows of bordered pits in radial and tangential walls. Vasicentric tracheids with 2 rows with distinctly bordered pits (fig. 6*I*).

Remarks. The combination of indistinct growth rings (2p), diffuse porous wood (5p), exclusively solitary vessels (9p), scalariform perforation plates with 22–42 bars (14p, 17p) opposite intervessel pits (21p, 22a), vessel-ray parenchyma pits with distinct borders (30p), vasicentric tracheids (60p), fibers with distinctly bordered pits (62p), nonseptate fibers (66p), multiseriate rays more than 4 seriate (98p) and that are not composed of only procumbent cells (104a) occur in four genera that belong to separate families and orders of eudicots: *Dillenia* (Dilleniaceae, Dilleniales), *Diplycosia* (Ericaceae, Ericales), *Microdesmis* (Pandaceae, Malpighiales), and *Styloceras* (Buxaceae, Buxales; InsideWood 2004–). Because this sample has features found in at least four genera, families, and orders, we refrain from proposing a formal name at this time and are following the approach Page (1981) took and referring to them only as a wood type.

Among Northern Hemisphere Cretaceous and Paleogene fossils, McRae angiosperm wood type 1 is most similar to DB.D1 Xylotype 2 from the Paleocene of the Denver Basin (Wheeler and Michalski 2003; InsideWood 2004–). It, however, is different from DB.D1 Xylotype 2, which has fewer vessels per square millimeter, rays of two distinct sizes, and sheath cells in some rays. McRae angiosperm wood type 1 falls into Page's group III–B2, characterized by pores mostly solitary, perforations scalariform, bars averaging less than 50. Axial parenchyma mostly apotracheal, vessel pits opposite-transitional (Page 1979, 1980, 1981). However, none of the 10 samples she assigned to this group have vasicentric tracheids.

The minimum axis diameter of the larger specimen is 21 cm. This indicates that the parent plant was a small tree or larger, depending on whether the specimen represents trunk wood or branch wood.

Discussion

The woods reported here expand our understanding of angiosperm diversity and physiognomy during the Late Cretaceous of the Western Interior of North America. *Laurinoxylon rennerae* represents the first wood record of Lauraceae from the Jose Creek Member of the McRae Formation. Leaves of Lauraceae are also present in the Jose Creek Member and comprise both pinnate and palmately veined taxa (Upchurch and Mack 1998). *Laurinoxylon rennerae* has a minimum axis diameter of 50 cm, which indicates that at least some Jose Creek Lauraceae were trees. Lauraceae have an abundant Cretaceous fossil record that includes leaf macrofossils, dispersed cuticles, permineralized and charcoalified wood, and reproductive structures (e.g., Drinnan et al. 1990; Upchurch and Dilcher 1990; Herendeen 1991; Upchurch 1995). In North America, lauraceous woods with oil cells are known from the late Campanian to Maastrichtian of California, New Mexico, and Mexico (Page 1967; Estrada-Ruiz et al. 2010).

Paraphyllanthoxylon, possibly Lauraceae but without oil cells, occurs in many Cretaceous wood floras (Gregory et al. 2009). Woods of some extant Lauraceae have the combination of features seen in *Paraphyllanthoxylon*, and there is one instance of a Cretaceous stem with *Paraphyllanthoxylon* anatomy attached to a lauraceous reproductive structure (Herendeen

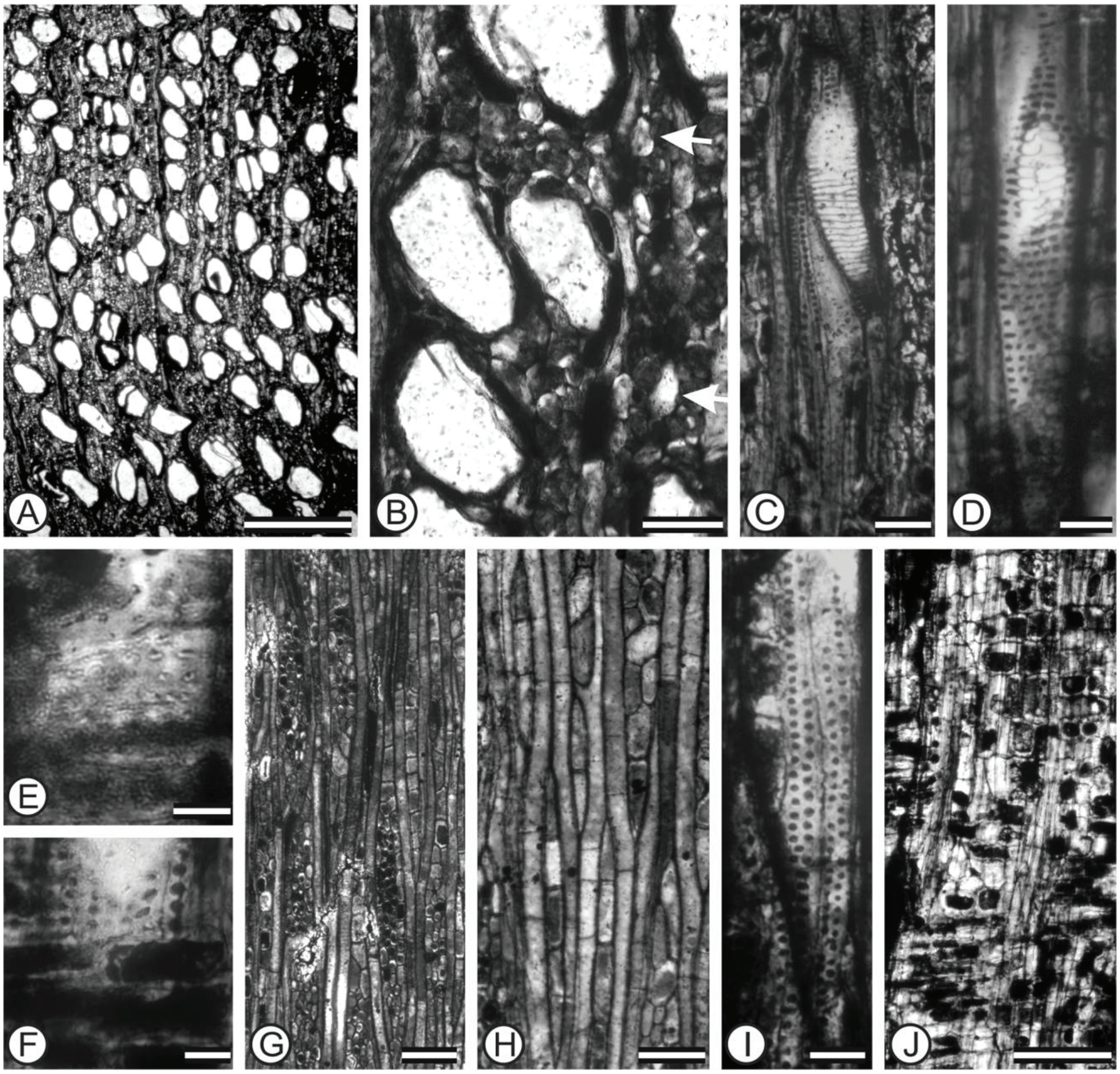

Fig. 6 McRae wood type 1. TXSTATE 1214. *A*, Transverse section (TS). Diffuse porous wood with solitary vessels. TXSTATE 1214–S2. Scale bar = 260 μm. *B*, TS. Solitary vessels, diffuse parenchyma (arrows). TXSTATE 1214-S2. Scale bar = 70 μm. *C*, Radial longitudinal section (RLS). Scalariform perforation plate, some bars are forked. TXSTATE 1214-S6. Scale bar = 60 μm. *D*, RLS. Opposite intervessel pits and scalariform perforation plate. TXSTATE 1214-S6. Scale bar = 32 μm. *E*, RLS. Vessel-ray parenchyma pits with distinct borders. TXSTATE 1214-S6. Scale bar = 14.5 μm. *F*, RLS. Vessel-ray parenchyma pits with distinct borders in procumbent ray cells. TXSTATE 1214-S6. Scale bar = 40 μm. *G*, Tangential longitudinal section (TLS). Multiseriate rays with cells of varying shapes. TXSTATE 1214-S5. Scale bar = 90 μm. *H*, TLS. Uniseriate and biseriate ray and parenchyma strands. TXSTATE 1214-S5. Scale bar = 75 μm. *I*, TLS. Vasicentric tracheids. TXSTATE 1214-S6. Scale bar = 35 μm. *J*, RLS. Heterocellular ray. TXSTATE 1214-S6. Scale bar = 120 μm.

1991). Recently, Jud et al. (2017) described a new species of *Paraphyllanthoxylon* from the Upper Cretaceous (Coniacian) Comox Formation on Vancouver Island. The tangential sections of the wood from the Comox Formation show rays with occasional inflated cells that have dark contents, suggesting oil cells and affinity with Lauraceae. Given the abundance of lauraceous leaves in the Late Cretaceous, it is probable that other Northern Hemisphere species of *Paraphyllanthoxylon* also are Lauraceae.

The eudicots described here cannot be placed with confidence in any single extant family. *Turneroxylon newmexicoensis* resembles two subfamilies of Dilleniaceae in most of its features but differs in having narrower rays. In *Turneroxylon*, multiseriate rays are no more than eight cells wide (generally up to six), while in similar Dilleniaceae, multiseriate rays are 10 or more cells wide (Dickison 1967, 1979). *Turneroxylon* shows similarity to other Cretaceous woods that have features found in Dilleniaceae (Page 1979, 1980). No leaves of Dilleniaceae have been validly identified from the Late Cretaceous of North America. This could simply reflect differences in the preservation of leaves and wood, but it also could reflect a lack of critical analysis of fossil leaves assigned to Fagales. Leaves of Fagales, such as *Ticodendron*, *Castanea*, and *Fagus*, show many features in common with those of Dilleniaceae (excluding *Hibbertia*) but differ in details of tooth structure and higher-order venation (Hickey and Taylor 1991).

Mccraeoxylon wadellii has a suite of features that occur in multiple orders. This situation finds a parallel with some woods (e.g., *Metcalfeoxylon*, *Sabinoxylon*, *Gregoryoxylon*) from other Cretaceous wood floras (e.g., Page 1981; Wheeler et al. 1995; Wheeler and Lehman 2000, 2009; Falcon-Lang et al. 2012). McRae angiosperm wood type 1 has a combination of features found in multiple extant orders of eudicots. Many of these characters are relatively primitive, according to the Baileyan model of wood evolution, and currently provide little clear evidence about relationships.

According to the Baileyan model of wood evolution (e.g., Bailey and Tupper 1918; Carlquist 1961), the presence of solitary and long vessel elements, exclusively scalariform perforation plates, fiber tracheids, and heterocellular rays is considered primitive/plesiomorphic in angiosperms. These characteristics are more common in Cretaceous woods than in Paleogene woods (Wheeler and Baas 1991, 1993). Of the eight types of fossil wood described from the McRae Formation, five have characters considered primitive, such as long vessel elements, scalariform perforation plates, and heterocellular rays. Only three types of fossil wood have characters considered derived/apomorphic, such as exclusively simple perforation plates (e.g., *Fulleroxylon*, *Pygmaeoxylon*, and *Mcraeoxylon*). These primitive characters seen in our woods are similar to what is found in other Western Interior wood floras, such as the San Juan Basin of New Mexico and Big Bend National Park, Texas (Wheeler et al. 1995; Hudson 2006; Boucher 2017).

The high incidence of these primitive characters in Cretaceous angiosperm wood floras relative to those of the Cenozoic might result from a narrower ecological niche for angiosperms during the Cretaceous (e.g., Wing and Boucher 1998) and/or early phylogenetic conservatism (Martínez-Cabrera et al. 2017). A large number of early angiosperms are known from mesic sites (e.g., Wing and Boucher 1998). Extant species with scalariform and oblique perforation plates have high prevalence in mesic environments such as tropical montane and temperate forests (Baas 1976; Carlquist 2001), where they are at less of a competitive disadvantage relative to simple perforation plates. Early phylogenetic conservatism could have restricted anatomical variation and niche expansion during the early phases of angiosperm evolution (Martínez-Cabrera et al. 2017), with a significant increase in plant size and hydraulic capacity occurring by the end of the Cretaceous (Upchurch and Wolfe 1993; Feild et al. 2011).

Lower-latitude wood floras have dicot woods with advanced characters not seen in more northern floras of similar age, suggesting that paleolatitude and paleotemperature were important factors in the evolution of angiosperm wood anatomy. For example, in the late Campanian (Estrada-Ruiz et al. 2013) wood flora of the Olmos Formation of Mexico there are three dicot woods with simple perforation plates, homocellular rays, and storied structure (*Javelinoxylon*, *Quercinium*, *Wheeleroxylon*; Wheeler et al. 1994; Estrada-Ruiz et al. 2010). As another example, the Campanian wood flora of the Hefhuf Formation of Egypt, located near the paleoequator, has multiple wood types with the advanced characters of vasicentric and banded axial parenchyma, despite low species diversity (Kamal El-Din 2003; Kamal El-Din et al. 2006). As a third example, the latest Cretaceous–earliest Paleocene Deccan wood flora, deposited in the tropical thermal belt (Smith et al. 2015), is remarkable for its essentially modern wood characteristics, such as a low percentage of scalariform perforation plates, a low proportion of exclusively solitary vessels, and a relatively high percentage of elaborate axial parenchyma patterns (Wheeler et al. 2017).

All described dicot woods from the McRae Formation have anatomical characteristics consistent with the tropical/warm subtropical temperatures and low-temperature seasonality inferred for the Late Cretaceous of the southern Western Interior (Wolfe and Upchurch 1987; Upchurch et al. 2015). For the Jose Creek flora, one climatically informative wood anatomical character is the absence of distinct and continuous growth rings in all species of angiosperm wood, which indicates little seasonality in temperature and the absence of winter dormancy. Reinforcing evidence for low-temperature seasonality is the presence of multiple types of palms in the Jose Creek wood flora (Estrada-Ruiz et al. 2012*b*) and multiple types of palms, cycads, and Zingiberaceae in the leaf flora (Upchurch and Mack 1998; Upchurch et al. 2017). The warm equable climate of the Jose Creek Member, in combination with the high diversity of the leaf flora and abundant preservation of fossil wood, suggests that future studies will reveal many new types of wood and make significant contributions to our understanding of the diversity of woody angiosperms during the Late Cretaceous.

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